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Population-ecology and migration of *Dero multibranchiata* STIEREN, 1892 (Naididae, Oligochaeta) in the Central Amazon inundation forest*

by

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Abstract

The influences of different substances on the population dynamics of the naeid *Dero multibranchiata* of the Central Amazonian inundated forests have been investigated. The most important factors are the kind of diet and the oxygen concentration. The speed of migration of the naeid species has been determined, which depends on the attractivity of leaf powder.

Keywords: Naididae, inundation forest, migration, population dynamics, Amazonia.

Resumo

Dero multibranchiata ocorre na floresta inundável da Amazônia Central. Em correlação com a enchente, a espécie acompanha a beira d'água e migra para o interior da floresta. Experimentos concernentes ao crescimento da população e a taxa migratória de *D. multibranchiata*, foram realizados em laboratório. O crescimento da população depende da composição do alimento. O crescimento máximo pode ser obtido pela mistura de barro e favelo de folhas. A concentração do oxigênio também tem forte influência no crescimento da população. A velocidade migratória aumenta, através da atração. A taxa de distribuição é de 6,7 cm/dia. Com a atração pelo farelo de folhas, a taxa média de migração aumenta para 24,6 cm/dia. A pressão d'água parece ter influência insignificante na taxa migratória. R-valores são também determinados para *Pristina longiseta* e *Alophorus carteri*. Dentre as três espécies de Naididae investigadas, *Pristina longiseta* apresenta a taxa máxima de reprodução.

*heartly dedicated to my former colleague Dr. H. Klinge at his 60th birthday.

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Introduction

The floodplains in Central Amazonia are subject to considerable water level fluctuations, averaging about 10.1 m during the course of the year. Wide areas along the shores are periodically inundated, bringing about the development of large wetland forests. A special feature of these Amazonian inundated forests is the seasonal periodicity of the flooding, which subjects the ecosystem to the dynamics of an annual cycle to a degree lacking in regions not subject to such flooding.

The seasonal occurrence of the flooding has a profound effect on the biotic communities of the water bodies in the region of the inundated forests along the Amazon and its tributaries. This is true for the benthic aquatic communities (REISS 1976a, 1976b) and floating meadows (JUNK 1973) in the standing water bodies as well as in the periodically flooded forests (IRMLER 1975). The growth of the vegetation is also forced into a seasonal pattern by the floods (JUNK 1970; WORBES 1985).

The animals in the inundated forests react to the flooding in different ways (IRMLER 1981; ADIS 1981, 1982, 1986). Migration is one of the most important escape mechanisms for both aquatic and terrestrial animals during inhospitable phases of the inundation cycle. These movements may follow the water line along the shore, or terrestrial animals may change their habitat from the ground to the branches of the trees (IRMLER 1979a, 1981; ADIS 1981, 1984).

There have been investigations of only a few terrestrial animal species to determine the physiological controls of the migrations. In some of these cases, direct contact with the water brought about a change in phototaxis, and in others, the temperature pattern, which is correlated with the water movements, was the trigger for the migration (IRMLER 1981, 1985). Aquatic animals also migrate in response to the water level fluctuations, but their physiological controls have not yet been investigated.

Due to their rapid population growth, oligochaetes in the family Naididae have special capabilities to react to water level changes by spreading into new aquatic habitats. It had to be determined to what degree these migrations are undertaken actively or whether the movements are random. These naids are particularly abundant in the temporary aquatic habitats along the Amazon and the Rio Negro (IRMLER 1977), where they are an important component of the species aggregations that break down the organic materials produced in the inundated forest (IRMLER 1979b). A study of naidid biology could therefore provide important information about the dynamics and function of the decomposition processes of the floodplain forests. This paper focusses especially on the species *Dero multibranchiata* (Fig. 1), which occurs in the mixed and black waters of the central Amazon region.



Fig. 1:
Hind part of *Dero multibranchiata*.

Results

1. Population-dynamics in the field

Field determinations of the population density of the species *Dero multibranchiata* were conducted in 1971 and 1972 (IRMLER 1975). They show that members of this species immigrate along the waterline in the flooded forests and develop their greatest population densities of 200 - 300 individuals per m² at depths from about 2 m to 3 m (Fig. 2). Within 4 or 5 months they may travel distances of 200 m or 300 m. *Dero multibranchiata* is a species of the inundated forests, which reaches its greatest population densities during the high water period and then suffers a population reduction during the low water phases.

Naidids can reproduce vegetatively by fragmentation of their bodies after chains of animals have been produced. MARCUS (1943) showed that a South American species *Dero evelinae* MARCUS, is able to regenerate the middle and hind part of the body in 8 days. It must therefore be assumed that the animals can reproduce vegetatively very rapid under favorable conditions. This suggest that *Dero multibranchiata* is an r-strategist with a high reproductive rate, and only because of this, it is capable of colonizing this kind of habitat as a pioneer species.

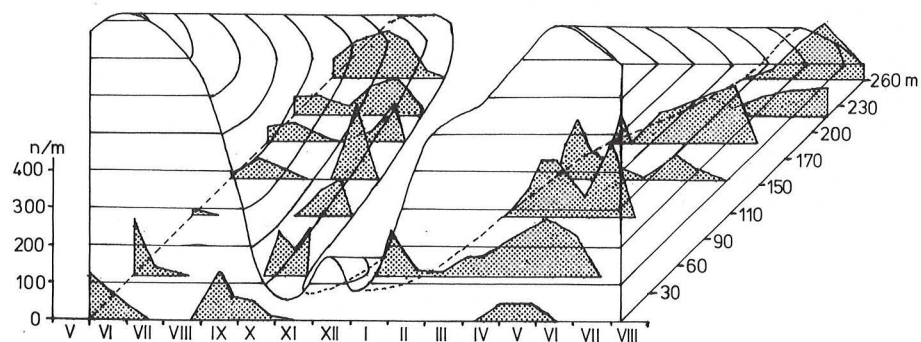


Fig. 2:
Population dynamics of *Dero multibranchiata* in correlation to the water level fluctuations. The data based on investigations from 1971/72 at Rio Tarumã Mirim near Manaus.

2. The regulation of the population growth

To verify the findings of the field investigations, experiments were undertaken to determine the population growth of *Dero multibranchiata* under various conditions and to see how well it conforms with the typical r-growth pattern. The aquaria for the experimental *Dero multibranchiata* were aerated, rectangular containers or jelly glasses maintained at 25 °C. Two individuals and sterilized sediment from their habitat were placed in each container.

Members of this species can easily be cultured on powdered nettle (Fig. 3). In containers to which no nettle powder was added, the population growth was so slight that it could be neglected. When nettle powder was added at regular intervals as a substitute for leaf litter, however, a significant increase in population density could be observed. Under these conditions, the growth reached its peak in about 40 days. After 80 days, the population in the containers cannot be maintained in spite of continued additions of nettle powder.

Analyses of the remaining substrate revealed that its condition had significantly changed. The substrate is ingested by the naids. The mixture of clay and nettle powder is released as faecal pellets after passing through the digestive tract. Apparently neither clay nor nettle powder alone can serve as a nutrient base for *Dero*.

The population decline may be due to the exhaustion of one of the nutrition components in the culture container: in this case the clay minerals. Another possible cause of the population decline in the containers is self-intoxication through the accumulation of faecal material.

Also investigated was the possibility that humic substances, from the pulverized leaves in the water, could stimulate the population growth. To do this, a culture container was supplied with Torumin peat-extract. The population growth observed, however, was similar to that in the containers to which no nettle powder was added. Humic substances can therefore be eliminated as the controlling factor for the population growth.

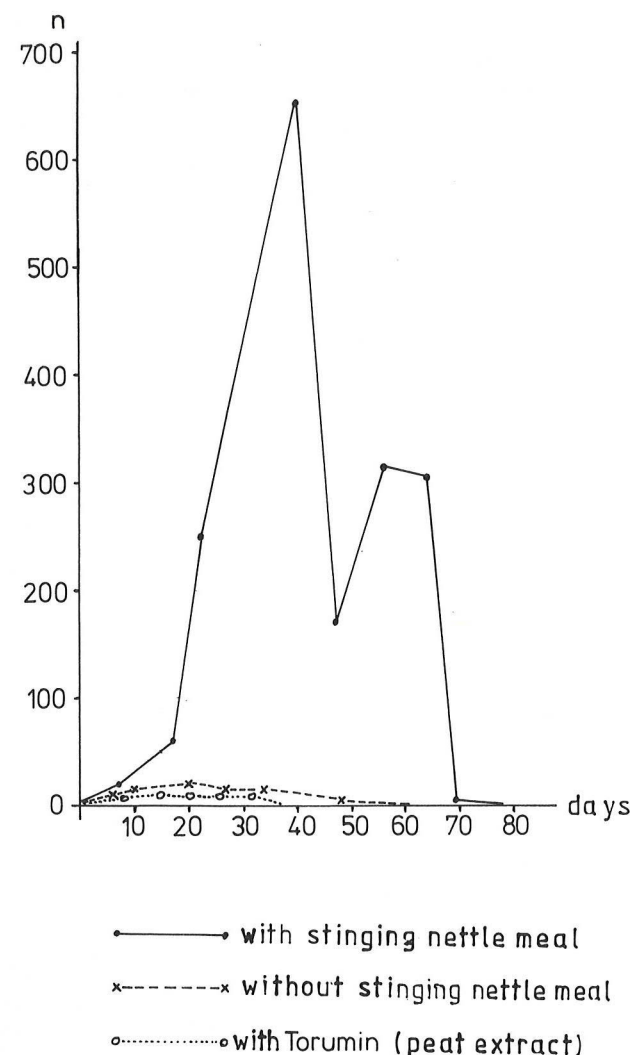


Fig. 3:
Population densities of *Dero multibranchiata* within 3 cultures with different nutrition conditions.

In its first phase, the population growth closely follows the curve of the differential equation, $dN/dt = rN$. The following r-values were obtained in the three experiments: $r = 0.17 \pm 0.03$ for the culture employing nettle powder, $r = 0.12 \pm 0.06$ for that without the nettle powder and $r = 0.08 \pm 0.01$ for the culture with peat-extract. After about 20 to 30 days, the population in all cultures begin to die off.

In order to investigate the effect the quantity of the leaf litter has on the population growth, a similar set of experimental conditions was established. The small aquaria were aerated, and sterilized, natural sediment was added. In each of them, 10 *Dero multibranchiata* individuals were placed, and different quantities of nettle powder were added in 7 parallel trials. After three weeks, the individuals in each container were counted.

According to the data obtained in these experiments, the rate, the population of *Dero multibranchiata* increases, depends on the food supply (Fig. 4). However, the increase in the growth rate continues only to about 100 mg per container; thereafter, it establishes a steady state. The variance in the population density of the individual trials is very great, so there are apparently other factors besides the quantity of leaf material that also significantly influences the population growth.

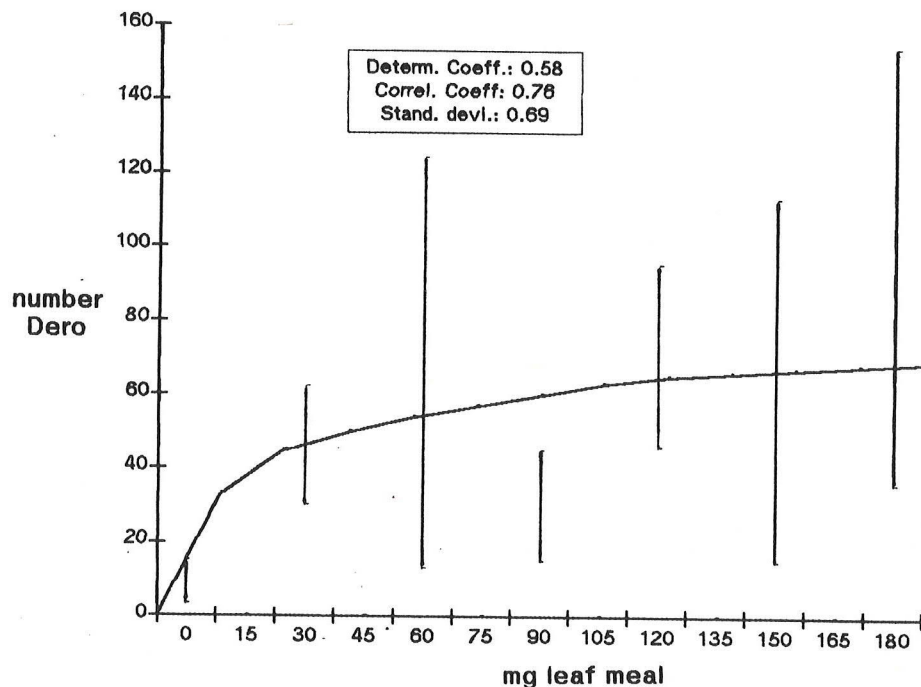


Fig. 4:
Correlation between the population density after 14 days and the nutrition amount by powdered nettles.

On the other hand, the growth phase in the cultures is not independent of the quantity of leaf material added. In one experiment involving the addition either 50 or 200 mg nettle powder per aquarium, the population growth of *Dero multibranchiata* was observed over a long period of time (Fig. 5). In the containers to which quantities of 50 mg of the leaf material were added, the maximum population density was reached after about 20-30 days. At that time, the population density in the containers to which 200 mg had been added was still lower than that in the aquaria receiving 50 mg. About 40 days after the beginning of the experiment, however, it had increased to about double that in the cultures receiving 50 mg per aquarium. It seems that the population growth begins more quickly in containers to which less leaf material is added.

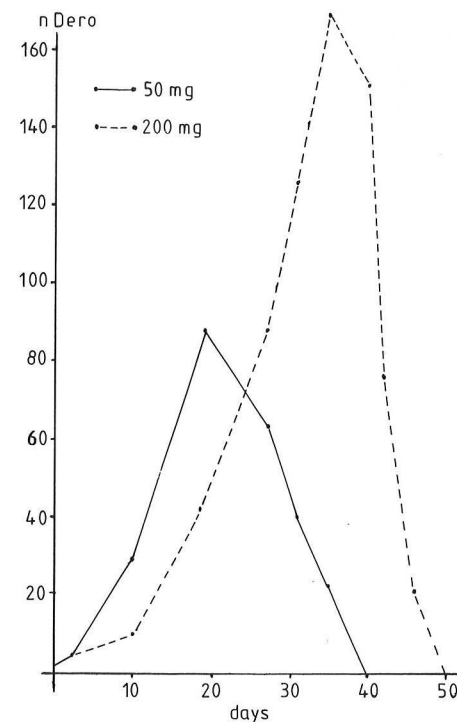


Fig. 5:
Population dynamics of *Dero multibranchiata* for two different amounts of powdered nettles.

The r-value for the cultures receiving 50 mg of leaf material per container was 0,19, while that for the culture receiving 200 mg per container was only 0,13. Even though the average r-value increase is slower in cultures receiving more leaf material than 100 mg per aquarium, the population increase continues for a longer period of time.

It was observed in the cultures that *Dero multibranchiata* builds small tubes out of substrate and prefers to remain on the bottom or sides of the aquaria. Therefore, the possibility that the surface area available for settlement influences the population growth was investigated. To do this, benthic plates for the containers were prepared to which a variable number of ribs, each 1 cm high, could be attached. The sterilized, natural sediment and 100 mg nettle powder were added to the aerated aquaria, and 2 *Dero multibranchiata* were placed in each. The population density was recorded after a period of 14 days.

The results depicted in Figure 6 show that a minor increase in the population can be induced by increasing the area of the surfaces suitable for settlement. However, a correlation cannot be statistically demonstrated.

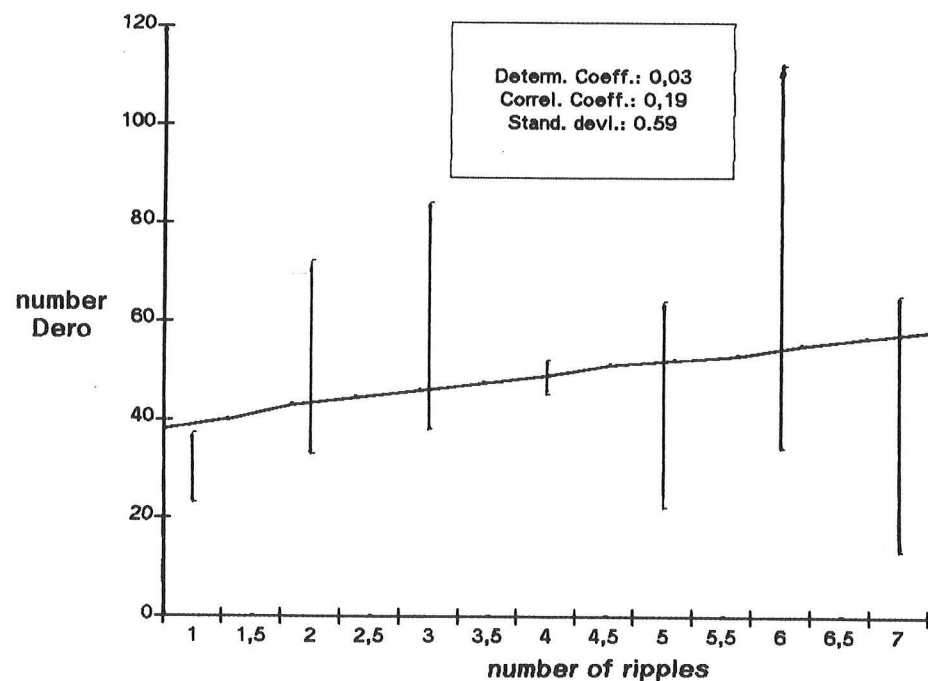


Fig. 6:
Correlation between the number of ribs on the bottom and the population densities after a period of 14 days.

Another experiment was undertaken to determine the influence of the oxygen content of the water on the population growth of *Dero multibranchiata*. For this, an elongated aquarium was divided into 7 compartments so that water could flow through only at the bottom. In these compartments, containers of sterilized sediment and powdered nettle were placed, and 2 *Dero multibranchiata* were released in each. On one side of the container was water saturated with oxygen, while on the other, sodium thiosulfate was added through a dropper. An outflow tube was placed in the middle (see also Fig. 8). After 14 days, the worms in the containers were counted. The oxygen content in each of the compartments was determined daily, and an average for the 14 days of the experiment was calculated.

As the data from this experiment show, the oxygen content has a very great influence on the population growth (Fig. 7). A comparison of the degrees of influences of three possible factors: the food supply in the form of leaf material, the surface area available for settlement, and the oxygen supply, shows that the 0.79 value for the influence of oxygen is greatest, while the effect of the surface area available for settlement on the population growth is practically negligible.

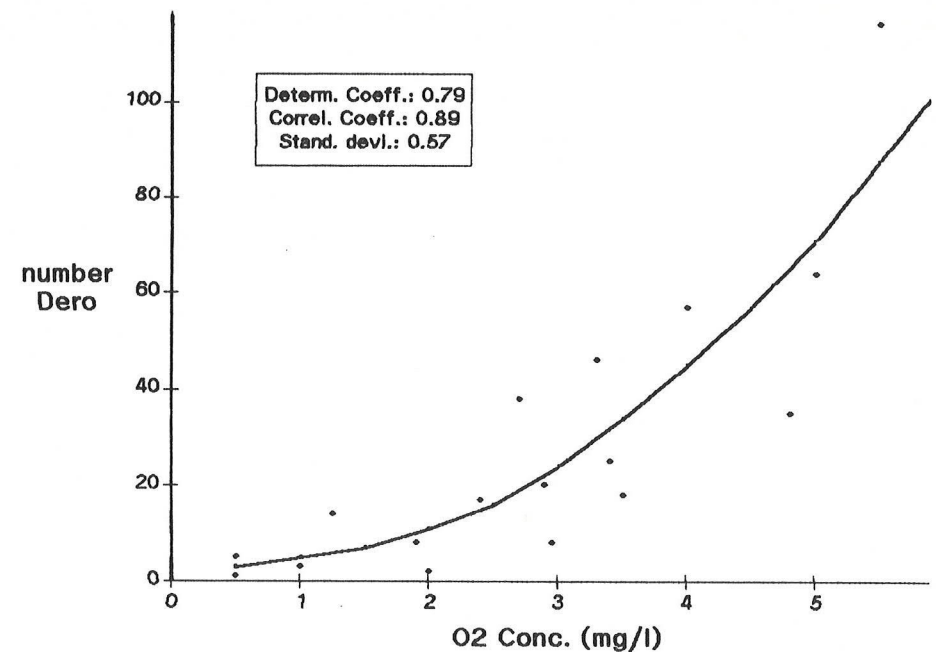


Fig. 7:
Correlation between the oxygen concentration and the population densities after a period of 14 days.

3. The regulation of the migratory behavior

The results of the field investigations and experiments on the population growth suggest that the r-strategist, *Dero multibranchiata*, is capable of quickly settling new habitats, and that the important factors contributing to the colonization include a source of oxygen and the presence of nutrients in the form of clay and leaf litter. In addition to the rapid rate of reproduction, various other factors might help accelerate the immigration into the inundated forests by attracting the worms.

To analyze the attraction exerted by various substances, that are released from the newly flooded forest into the littoral zones of the river, the following experiment was conducted. Seven containers were placed on the bottom of 45 x 4 cm aquarium in which an evenly distributed layer of sterilized, natural sediment had been placed. A gauze bag containing leaf litter was placed at one end of the aquarium during each test. At one end of the aquarium, the material to be tested was introduced, and at the other was an inflow of freshwater. Water was drained from the center of the aquarium so that a gradient could be established between the test substance and the fresh water. At the start of the experiment, 100 *Dero multibranchiata* were placed in the center container, and after one day of exposition to the test substance, the number of worms in each of the seven containers was determined.

The results of the various trials are depicted in Figure 8. In addition to both varieties of leaf litter tested, powdered leaf litter from the inundated forest, nettle powder, sodium

glutamate, and glutamic acid attracted the worms. The other substances tested exerted no demonstrable attraction or acted as repellents, as in the case of cumarin. Even the humic substances in Torumin peat extract did not attract the worms, although this might have been expected, considering that humic acids would be released from the flooded forests. The chemical attraction of leaf litter and glutamic acid suggest that the bacterial decomposition of the leaves during the flood phase attracts the worms. This is especially likely since naids can nourish themselves directly from bacteria (LEARNER et al. 1978).

In addition to the chemical attraction produced by the bacterial decomposition of the leaf litter, the migration might have been influenced by physical factors. The increase in the water pressure resulting from the rising water level might be important for triggering the migration. In order to test this possibility, a pressure chamber 50 cm long was constructed, in which a staircase for seven containers was covered with sterilized, natural sediment. An air pump connected to the chamber through a valve was used to set the desired pressure in the uppermost container. Because of the height of the steps in the staircase, the pressure in the container at the bottom of the pressure chamber was about 0.05 atmospheres greater than that in the uppermost level. At the beginning of each experiment, 100 *Dero multibranchiata* were placed in the middle container, and one day later, the worms in each of the 7 containers were counted.

From the data obtained in these trials (Fig. 9), it can be assumed that under the given experimental conditions, a migration is induced only after the pressure on the worms has increased to that encountered beneath a 5 m water column. In this case, the migration is undertaken only to escape exposure to still higher pressures. By lowering the pressure, no migration into deeper water could be provoked. Because the containers on the bottom were arranged on a staircase, the actual effects of the water pressure could not be fully expressed. Possibly, a migration along an inclined plane could have been induced by a lower pressure than those applied in the test.

Because of the discontinuity of the benthic profile during the pressure test, determining the speed of the migration was not possible. This could be measured in the small elongated aquarium, however. To do this, sterilized, natural substrate was placed in the 7 containers, which are again set out on the floor of the aquarium. A container at one end of the aquarium was stocked with 100 *Dero multibranchiata*, and after a certain period of time, the worms in each of the 7 containers were counted.

In order to investigate the influence of the leaf litter on the rate of migration, a gauze bag containing leaf powder was hung at the end of the aquarium opposite the container in which the *Dero multibranchiata* were placed. This leaf material had been left in water for about two days before start of the experiment in order to permit bacterial decomposition to begin and thereby increase the attraction. With this experimental arrangement, an increase in the speed of the migration resulting from the presence of powdered leaves was demonstrated (Fig. 10). While only a slight shift in the location of the population was observed when no powdered nettles were added, the addition of the powder effected the immediate initiation of a migration in its direction. After one day, nearly the entire population had already travelled to the location of the powdered nettles.

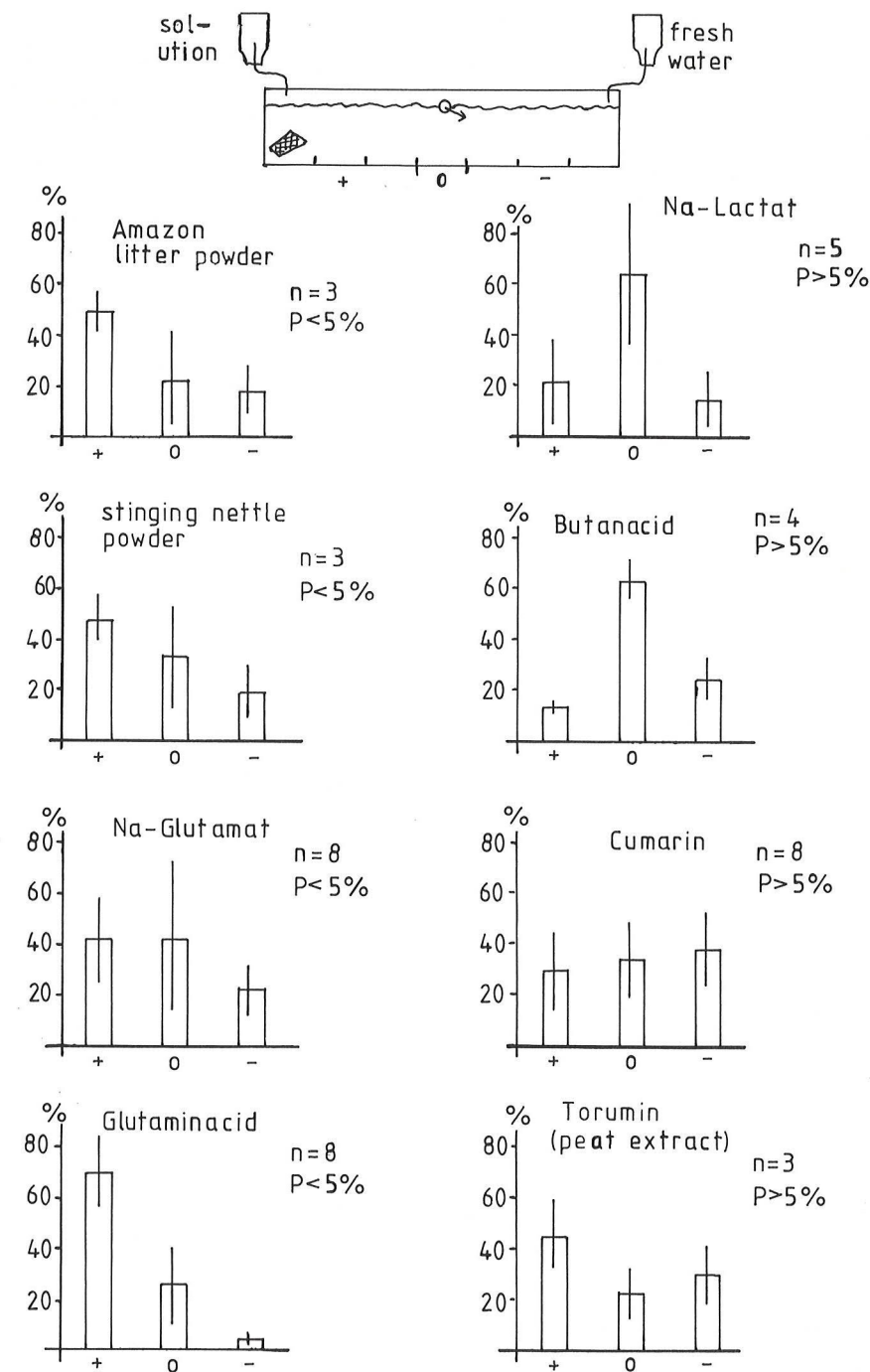


Fig. 8: Attractivity of both different leaf powders and solution respectively on *Dero multibranchiata*. Further description of the experiment see text.

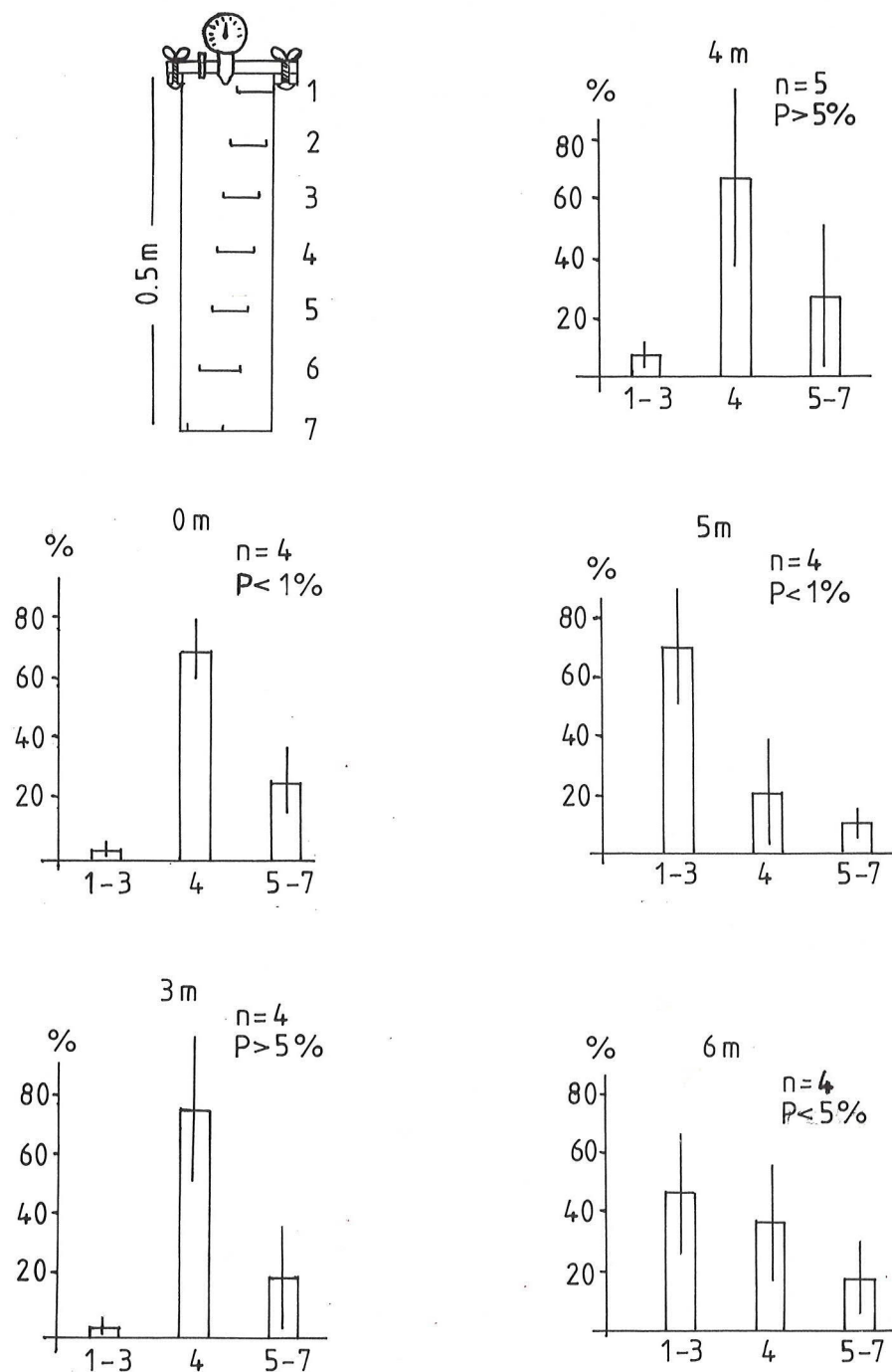


Fig. 9:
Migratory behaviour based on an increasing water pressure. The animals were placed in part 4 and the migration into the other parts was studied by counting the number of individuals in all compartments after a period of 1 day.

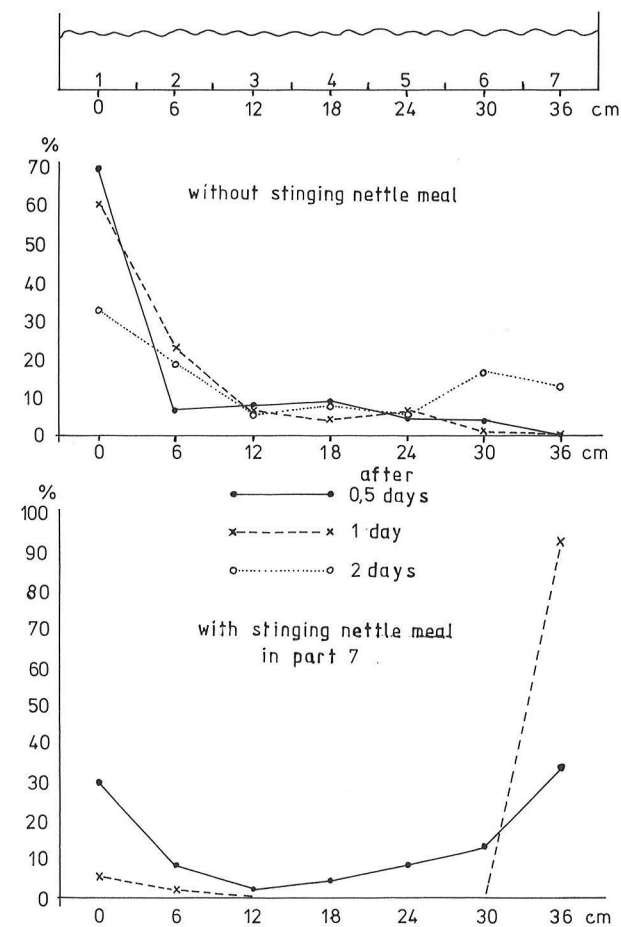


Fig. 10:
Migratory behaviour of *Dero multibranchiata* in an elongated aquarium. Worms are either attracted by leaf powder or they are not attracted.

The speed of the movement could be calculated by the following formula

$$W = \frac{\sum_{i=6}^{36} m \cdot i}{M}$$

(W = mean migration speed of the population in cm/day, m = number of worms/container, M = total number of worms and i = distance travelled in cm) (Fig. 11). The normal speed at which *Dero multibranchiata* spreads when no supplemental attraction is exerted by leaf litter was found to be 6.7 cm/day in this experiment. This is only 27 % of the speed that can be reached when leaf litter provides a supplemental attraction. The period of increasing water levels in Central Amazonia can last for about 5 months, and during this period, the inundated forests are available for the immigration of *Dero multibranchiata*. According to the data obtained in this experiment, 50 % of the population would have migrated only 36.9 m into the forest. However, 5 % of the population would have already migrated a

distance of 368.8 m. Therefore, only a small part of the original population can be responsible for the formation of the population along the shores of the inundated forests, even if the added stimulus of an increasing water pressure, which was ignored in these experiments, is incorporated into the calculations.

nettle powder	n	w	s	p
—	5	6.7	1.4	
+	3	24.6	10.6	< 5 %

migration within 5 months (m)				
nettle powder	w 50 %	w 30 %	w 10 %	w 5 %
—	10.1	16.7	50.1	100.0
+	36.9	55.4	184.5	368.8

Fig. 11:
Mean speed of migration of *Dero multibranchiata* for different attraction conditions and the migration of different percentages of the population within 5 months.

Can an immigration by *Dero multibranchiata* into the inundated forest be modelled based on its population dynamics and tendency to be attracted to certain substances? From a modification of the formula for the speed of migration, the percentage of the population that has reached a given location from the starting point can be calculated:

$$wp = t \cdot e^{w \cdot k} \cdot \ln p$$

(wp = distance from the starting point in m, t = time in days, w = speed of migration, k = constant and p = the percentage of the population) (Fig. 12).

In order to simulate the development of the population in the field, several conditions must be fulfilled. Because the mortality was not determined, the findings of SCHÖNBORN (1985) were utilized. He estimated a mortality of 52 % in 14 days for naidids. Because the population growth is dependent upon the oxygen concentration, the dependence was calculated based on the experimental findings. The oxygen concentration in the deep water at the Rio Tarumã Mirim, where the investigation was conducted, depended on the level of the water. It decreased from about 5.0 mg/l to 0.5 mg/l while the water was rising between January and July (Fig. 13). Another unknown factor for the simulation of the migration is the capacity of the habitat to support *Dero multibranchiata*, expressed as the number of worms per unit area. To calculate this factor, the arbitrary supposition was made that for 1000 individuals the r-value would be negative and equal -0.07 respectively for 10000 individuals equal -0.17.

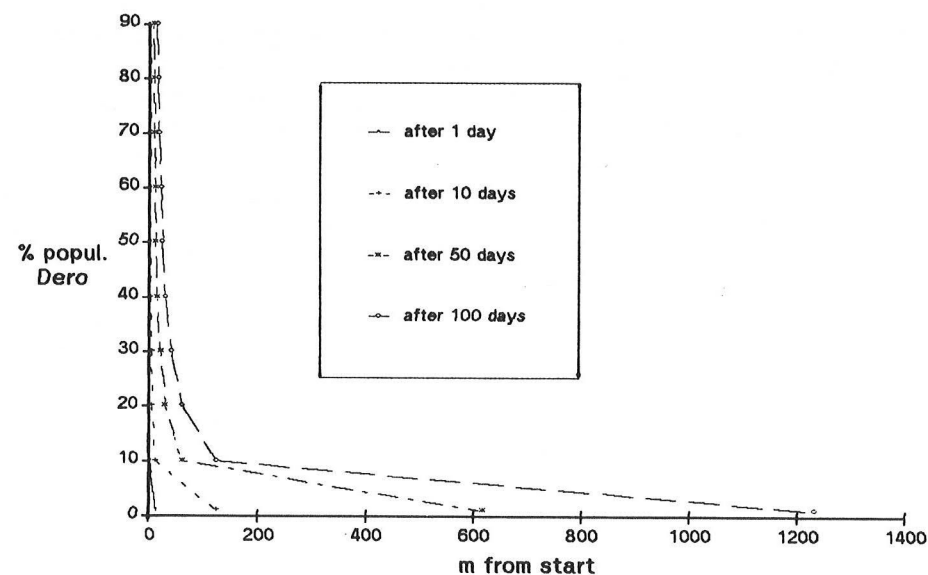


Fig. 12:
Migrations of different parts of the population of *Dero multibranchiata* based on the calculated migration rate under the condition of an attraction by leaf powder.

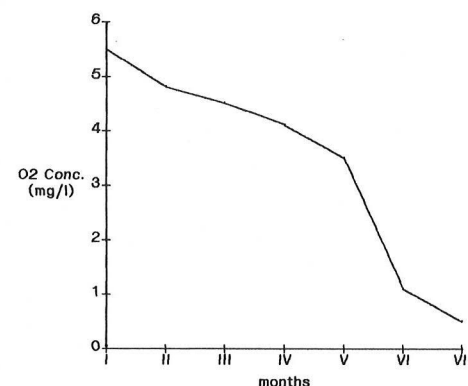


Fig. 13:
Oxygen concentration in the inundated forest based on data from Rio Tarumã Mirim in 1971/72.

Based on the above assumptions, the course of population growth at two different locations in the inundated forest can be calculated. At the first location, the growth of the population from an initial stock of two worms in January continued for 180 days until June. The mortality should have been 60 % in 10 days, the emigration should have amounted to 99 %. There should have been no immigration. The curve A is depicted in Fig. 14. It shows that during the early phase, the losses from mortality and emigration are great enough to keep the density of the population very low. Later on, a significant increase in the population density occurs, which is limited first by the capacity of the habitat to support the population and then by a decrease in the oxygen concentration. At the second location, the initial population is assumed to be 0.1 worm. Again, the mortality is assumed to be 60 %, and there is an immigration of 0.1 individual/day and no emigration. The population is then allowed to grow for 90 days. Assuming these conditions, the curve B in Fig. 15 was plotted. It shows that the population begins immediately to grow rapidly, and it is limited only by the capacity of the habitat to support it.

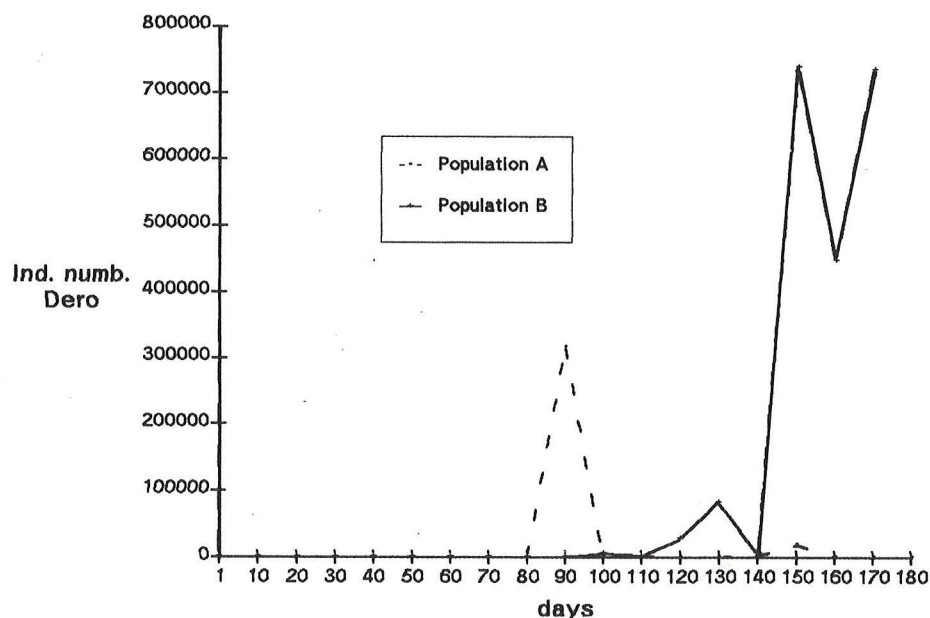


Fig. 14:
Simulated population densities for two populations of *Dero multibranchiata* both the near river forest (population A) and the high inundation forest (population B) respectively. Arbitrary assumptions see text.

4. Influence of the competition in the population dynamics of *Dero multibranchiata*

Dero multibranchiata occurs in the flooded regions investigated together with other nauid species, including *Pristina longiseta* and *Dero (Aulophorus) carteri* STEPHENSON. Both of these species were studied to detect influences that they might have on the population of *Dero multibranchiata*. To do this, two *Dero multibranchiata* and two of each of the other species were placed in a small aquarium to which sterilized, natural sediment and powdered nettles had been added, and the development of the populations was observed (Fig. 15).

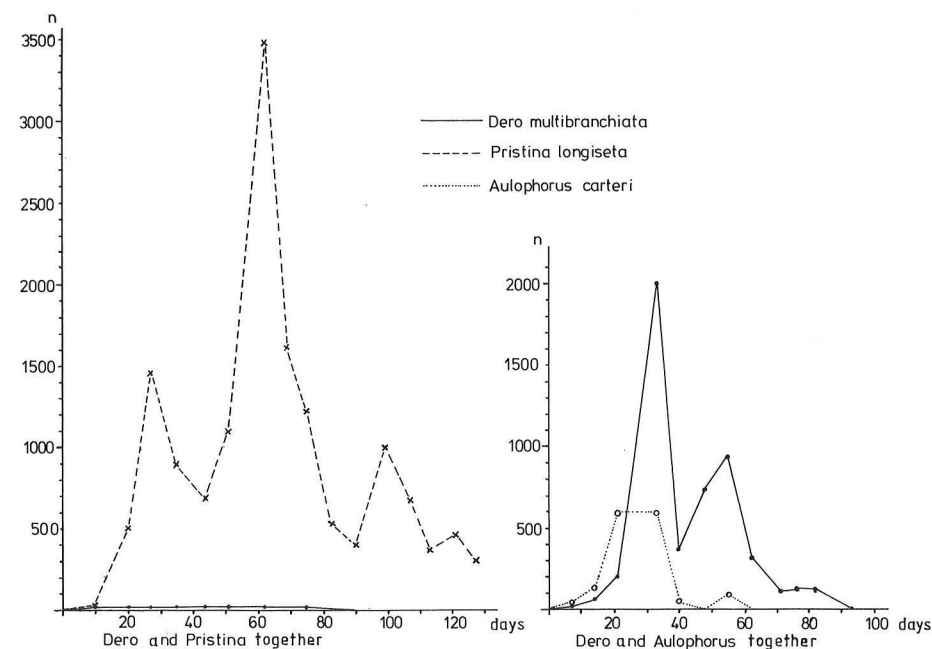


Fig. 15:
Population dynamics of *Dero multibranchiata* in a culture with two other nauid species together.

In a culture with *Pristina longiseta*, *Dero multibranchiata* cannot form a large population, because *Pristina longiseta* is a stronger competitor. This is certainly partly due to its more rapid reproduction rate. While *Pristina longiseta* is able to produce a population of 500 individuals in only 20 days, *Dero multibranchiata* can multiply to only between 50 - 100 worms in that time, even under optimal conditions in the cultures. The degree to which the suppressive influence of *Pristina* on its consumption of the food has still not been determined. In spite of its high fluctuations, the population of *Pristina longiseta* seems to be more stable than that of *Dero*. Furthermore, the population fluctuations of *Pristina longiseta* may be caused by methodological errors, since only representative samples were counted due to the large population size. Although *Dero multibranchiata*

populations could not be maintained in cultures longer than 2 1/2 months, those of *Pristina longiseta* could be kept for 1/2 year in cultures without difficulty. The speed of migration by *Pristina*, which is uninfluenced by an attraction to leaf litter, is only 3.9 ± 1.6 cm/day, significantly lower than that of *Dero multibranchiata*.

In competition to the second naidid species, *Dero (Aulophorus) carteri*, *Dero multibranchiata* seems more successful. *Aulophorus carteri* was considered by REISS (1976b) to be a species of the surface layer, or limnokinetic, in the várzea lakes of Amazonia. As the culture experiment showed, *Aulophorus carteri* also requires an addition of powdered leaves, especially since worms of this species build small cases out of leaf fragments to conceal themselves in. In the cultures, *Aulophorus carteri* certainly did not confine itself to the surface layer but rather seemed to prefer the bottom layer and the walls of the aquaria for settlement.

In spite of the apparently higher reproductive rate of *Aulophorus carteri*, *Dero multibranchiata* is able to successfully develop in the combined culture, and 1 1/2 months, it is able to eliminate the competitor. The occupation of niches by these three naidid species in the field supposedly depends on their mutual abilities to eliminate each other. The strongest competitor, *Pristina longiseta*, can eliminate the other two species because it has the highest r-value. The three species have the following r-values:

<i>Dero multibranchiata</i>			
with powdered nettles		without powdered nettles	
r-value	doubl. rate	r-value	doubl. rate
0.17 ± 0.03	3.1	0.12 ± 0.06	6.3
with powdered nettles			
<i>Pristina longiseta</i>		<i>Aulophorus carteri</i>	
r-value	doubl. rate	r-value	doubl. rate
0.33 ± 0.14	3.3	0.18 ± 0.02	2.8

Aulophorus and *Dero* have r-values that are about equal. Because of its capability to build cases out of leaves, *Aulophorus* is able to provide itself with greater protection, especially against the solar radiation, and gain access to the air. This gives it the capability of also settling in the surface layer of the water. Among the three species investigated, *Aulophorus carteri* seems to have the weakest competitive potential, so the surface of the water seems to be a refuge habitat for the species. *Dero multibranchiata* finds its ecological niche in the inundated forests due to the speed of its migration and the attraction exerted on it by leaf litter.

Discussion

The Naididae is a widespread family in South American water bodies. The species investigated, *Dero multibranchiata*, is known from all parts of South America from Trinidad to Argentina (DI PERSIA 1980) and has been found both in small water bodies and in streams and rivers. There have still been no investigations on the kinds of water bodies this species inhabits or their water level fluctuations, so it is not possible to make a comparison of the flooded forests and other kinds of South American habitat. From the biology of the species, it is suspected that it prefers water bodies with water level fluctuations and a good supply of dissolved oxygen.

The population density of naidids can be very great. For the river Elbe (West Germany), PFANNKUCHE (1981) reported densities between 1000 and 78 000 ind/m². LEARNER et al. (1978) found the maximum population densities of individual species in British waters to be between 500 and 5000 ind/m². In a subtropical black water river in the U.S.A., the number oligochaetes averaged about 1000/m² (BENKE et al. 1984). In the Amazonian forests flooded by black waters, the population density of naidids is relatively high, ranging from about 500 to 10 000 ind/m² (IRMLER 1975). This figure is even higher than that in white waters and river lagoons (REISS 1976a).

The development of naidid population is characterized by large seasonal fluctuations in population density (LEARNER et al. 1978; PFANNKUCHE 1981). Because of their potential for rapid reproduction through budding or fission, these worms can colonize a location rapidly. According to LODEN (1981), naidid species from unstable ecosystems can also settle ecosystems with stable condition but not vice versa. Therefore, unstable ecosystems can be characterized by their naidid fauna. Under favorable conditions, reproduction is normally asexual. Sexual reproduction begins to occur as the conditions deteriorate, such as through desiccation (MEHRA 1920). Therefore, it was suspected that the species from unstable ecosystems would be especially likely to have the capability for sexual reproduction (LODEN 1981). On the other hand, PFANNKUCHE (1981) encountered sexually mature individuals mainly during population maxima. We were unable to find any sexually mature *Dero multibranchiata*, either in the field or in the culture.

The reproduction rates of naidid species are still poorly known. Because they are dependent upon temperature (LOCHHEAD & LEARNER 1983; McELHONE 1978; SCHÖNBORN 1985), it is assumed that the rates for tropical species would be high. The r-values reported by LOCHHEAD & LEARNER (1983) are slightly lower for a temperature of 20 °C than those found for *Dero multibranchiata* and *Aulophorus carteri* at 25 °C, so similar reproduction rates can be assumed. However, the r-value for *Pristina longiseta* is considerably higher than any other previously known. In contrast, the doubling rate of 8 days for *Dero evelinae* determined by MARCUS 1943 is relatively low; however, no information on the temperature was provided. The rate of division may decrease again after temperature optimum has been passed (VAN CLEAVE 1937). It seems that the fission rate reaches maximum values for tropical species like *Pristina longiseta* at 25 °C degrees (VAN CLEAVE 1937).

With few exceptions, naidids feed on detritus or algae (LEARNER et al. 1978; HARPER et al. 1981b; BEWKER et al. 1983). The choice of food can contribute to eco-

logical differentiation, even among coexisting species (McELHONE 1979). Algae feeders seem to choose their food opportunistically without showing selectivity, but their local population densities seem to be dependent on the kind of food available (BAKER & BRADNAM 1976). According to HARPER et al. (1981a), about 99 % of the bacteria are digested during a passage through the digestive tract lasting about 39 minutes.

The great majority of the species in the genus *Dero* seem to consume detritus, and only a few feed on algae (GRIMM 1981). The naids in the inundated Amazonian forests seem to consume fungus spores as well as detritus (IRMLER 1975). *Dero multibranchiata*, however, must have mineral substances as well as organic detritus available, because neither one nor the other component of the diet alone will support the optimal population growth. The reason for this situation are still unknown. Supposedly, besides the digestion of the bacteria and fungus spores, the consumption of trace elements in the clay is a requirement of the worms.

Bacteria and fungi are the main agents decomposing the leaf litter beneath the flood waters (KAUSHIK & HYNES 1971; SUBERKROPP & KLUG 1976). It is therefore probable that bacteria and fungi consumers would be attracted by decomposing leaf litter. This has already been demonstrated for oligochaetes in the family Tubificidae (LAZIM & LEARNER 1987). Tubificidae can also distinguish different grades of water quality and migrate to locations where their preferred conditions prevail (ZAHNER 1967). *Dero multibranchiata* also seems to be attracted by leaf litter being decomposed by bacteria and fungi. In this case, it is mainly glutamine that is responsible for the attraction. However, glutamine alone attracts the worms less than decomposing leaves, so additional substances must also contribute to the attraction.

How can we interpret the migratory behaviour of *Dero multibranchiata*? No additional data from other investigations are available. *Dero multibranchiata* seems to be attracted by the glutamine formed during the decomposition of the leaf litter. As the water level increases, more and more areas of the forest are flooded, and the substances in the leaf litter that attract the worms enter the water and attract *Dero* deeper into the forest. Because of the ample food subby in the newly flooded regions, an optimal population growth is supported, while in the parts of the forest that have been under water for longer periods of time, the living conditions for the worms deteriorate to a lowering of the oxygen concentrations. Besides chemical attractants, the physical stimulus of the water pressure seems to play a role in the migration. Due to the both kinds of stimulus, the immigration into the forest occurs relatively rapidly. For the return migration, an attraction to decomposing leaf litter cannot be a factor. This can occur at the normal wandering rate of the species, perhaps somewhat supported by a reaction to water pressure. Therefore the return migration is apparently slower than the immigration into the forest, and the losses to the population are greater. Therefore, the population density would again be low.

Summary

Dero multibranchiata occurs in Central Amazonian inundation forests. The species migrates into the forest in correlation with the water level fluctuations. Laboratory experiments were executed concerning the population growth and the speed of migration of *Dero*. The population growth of *Dero* depends on the composition of its diet. An optimal growth can be obtained for a mixture of clay and powdered leaf litter. Furthermore the oxygen concentration strongly influences the population growth. The speed of the migration increases, if worms are attracted by powdered leaves. The distribution rate amounts to 6.7 cm/day. As worms are attracted by powdered leaf litter, the average speed of migration increases up to 24.6 cm/day. The water pressure seems to have only a weak influence on the speed of the migration. R-values are also determined for *Pristina longiseta* and *Aulophorus carteri*. *Pristina longiseta* has the highest reproduction rate of the three investigated naidid species.

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